

Ergatomorph wingless males in *Technomyrmex vitiensis* Mann, 1921 (Hymenoptera: Formicidae)

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Abstract

Ergatomorph wingless males are known in several species of the genus *Technomyrmex* Mayr, 1872. The first record of these males is given in *T. vitiensis* Mann, 1921. In comparison with winged males, wingless males have a smaller thorax and genitalia, but both forms have ocelli and the same size of eyes. Wingless males seem to form a substantial portion (more than 10%) of all adults in examined colony fragments. Wingless males are present in colonies during the whole year, whereas the presence of winged males seems to be limited by season. Wingless males do not participate in the taking care of the brood and active foraging outside the nest. Males of both types possess metapleural gland openings. Beside males with normal straight scapes, strange hockey stick-like scapes have been observed in several males. The cause of this divergence is unclear.

Keywords

Behaviour, biology, greenhouses, *Technomyrmex vitiensis*, wingless ergatomorph males

Introduction

Two morphs of males evolved independently in several ant genera, such as *Cardiocondyla* Emery, 1869 (Heinze et al. 2013), *Hypoponera* Santschi, 1938 (Bolton and Fisher 2011), *Plagiolepis* Mair, 1861, *Crematogaster* Lund, 1831, *Formicoxenus* Mayr, 1855, *Pheidole* Westwood, 1839 (Heinze and Tsuji 1995) and *Technomyrmex* Mayr, 1872 (Bolton 2007). *Technomyrmex* ants display a unique mode of reproduction. In *Technomyrmex*, wingless intermorphic females are known in more than 25 species and wingless ergatoid males in six species (Bolton 2007). In the well-known species *T. brunneus* Forel, 1895 (Tsuji et al. 1991, Yamauchi et al. 1991, Tsuji and Yamauchi 1994, Ogata et al. 1996), winged queens and males are produced and mate synchronously once a year and each winged female tries to found a new colony independently. Later on, as the colony grows, the foundress is replaced by fertile apterous intermorphic females, which mate with their brothers, apterous ergatoid males. The genitalia of winged reproductives are significantly bigger than the genitalia of apterous individuals. Thus, the copulation between winged and wingless reproductives seems complicated or impossible (Ogata et al. 1996). The colony spreads by budding, forming a huge polycalic colony with thousands of individuals.

Technomyrmex vitiensis Mann, 1921 is probably of South-East Asian origin, but recently has been found to be widespread in greenhouses across the whole world (Bolton 2007, Pospischil 2011). Despite its worldwide distribution, its biology is poorly known and it is considered to be similar to its more intensively studied relatives from the *Technomyrmex albipes* species group such as *T. brunneus*, *T. pallipes* (Smith, 1876) and *T. difficilis* Forel, 1892. According to Bolton (2007), *T. vitiensis* nests in various materials and spaces such as in leaf litter, under stones, on vegetation in twigs or under leaves. It tends homopterans for honeydew and preys on small arthropods. Wingless males are not known in *T. vitiensis* although they occur in several related species (Bolton 2007, Oettler and Heinze 2009). Because of the absence of wingless males in studied colonies, Oettler and Heinze (2009) proposed the reproduction of *T. vitiensis* via thelytocous parthenogenesis.

In this paper, the presence of wingless ergatomorph males of *T. vitiensis* is described.

Methods

Two populations of *T. vitiensis* were discovered in the Czech Republic in the autumn of 2014: one in the greenhouse of the botanical garden of Charles University (Czech Republic, Praha, 50°4'N, 14°25'E; 8.10.2014, lgt., det. et coll. P. Pech, revid. et coll. B. Bolton) and another in the greenhouse of the Prague Zoo (Czech Republic, Praha, 50°7'N, 14°24'E; 23.9.2014; lgt., det. et coll. P. Pech). Collections of individuals and observations of the behavior of ants in the greenhouse of the botanical garden were carried out from the beginning of October 2014 to November 2015. Two colony fragments were collected and preserved in pure ethanol, one in the botanical garden in November 2014 and the other in zoological garden in November 2015.

The morphology of ants was examined using a JEOL JSM-7401F electron microscope and a binocular microscope with 40× magnification. Differences in morphometry between winged and wingless males were analyzed using the Mann-Whitney U test and the correlation between thorax length and width of genitalia was tested by Spearman rank-order correlation. Six winged and 12 wingless males were examined. The following characteristics were measured:

| | |
|-----------|--|
| HW | Head width; maximum width of cephalic capsule with eyes, measured in full-face view; |
| HL | Maximum length of head; length of cephalic capsule measured in full-face view in midline from anterior margin of clypeus to posterior head margin; |
| MH | Mesosoma height; maximum height of mesosoma from ventral margin of mesopleuron to dorsal margin of metanotum, measured in lateral view; |
| ML | Mesosoma length; maximum length measured from anterior margin of pronotum to posterior margin of propodeum, measured in lateral view; |
| SL | Scape length; maximum length of single scape, measured along outer edge; |
| EL | Eye length; maximum length of single eye; |
| EW | Eye width; maximum width of single eye perpendicular to EL; |
| GW | Genitalia width; maximum width of genital capsule (sensu Boudinot 2013), measured in dorsal view. |

To observe behavior and reproduction, one colony fragment was collected in the botanical garden and reared in captivity at room temperature and with a natural photoperiod from November 2014, first in a plastic box (30×20×10 cm) and later in a petri dish (10 cm in diameter). The walls of both containers were coated in baby oil to prevent escape. The ants were fed with honey and pieces of insects. Another colony fragment was collected in the zoological garden in November 2015. It was reared under the same temperature and photoperiod, but kept in a glass terrarium (30×20×20 cm) situated in a flat plastic container with water. These ants were fed by Bhatkar and Whitcomb (1970) diet.

Results

Morphology

Beside the presence or absence of wings, the architecture of the thorax is the most obvious difference between males of both types (Tab. 1). The thorax of a winged male is high and large due to the presence of wing muscles whereas the smaller thorax of the wingless male resembles a worker (Fig. 1A, B) at first sight. Moreover, thoraces of winged males are longer. Males of both types have ocelli and similar head morphology (Fig. 1C; Tab. 1). The width of male genitalia is positively correlated with the length of the thorax ($n = 18$, $R = 0.82$, $p < 0.01$).

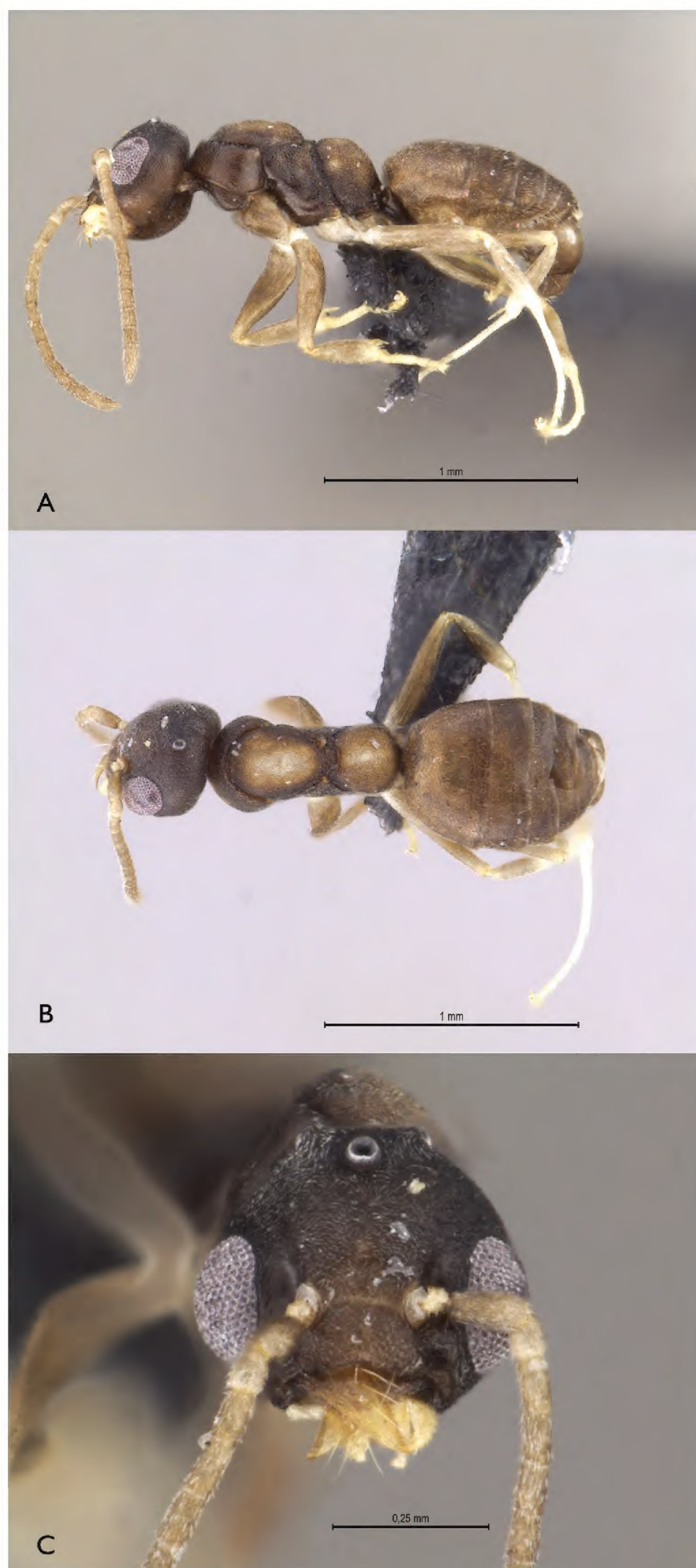


Figure 1. Lateral (A), dorsal (B) and frontal (C) view of wingless *T. vitiensis* male.

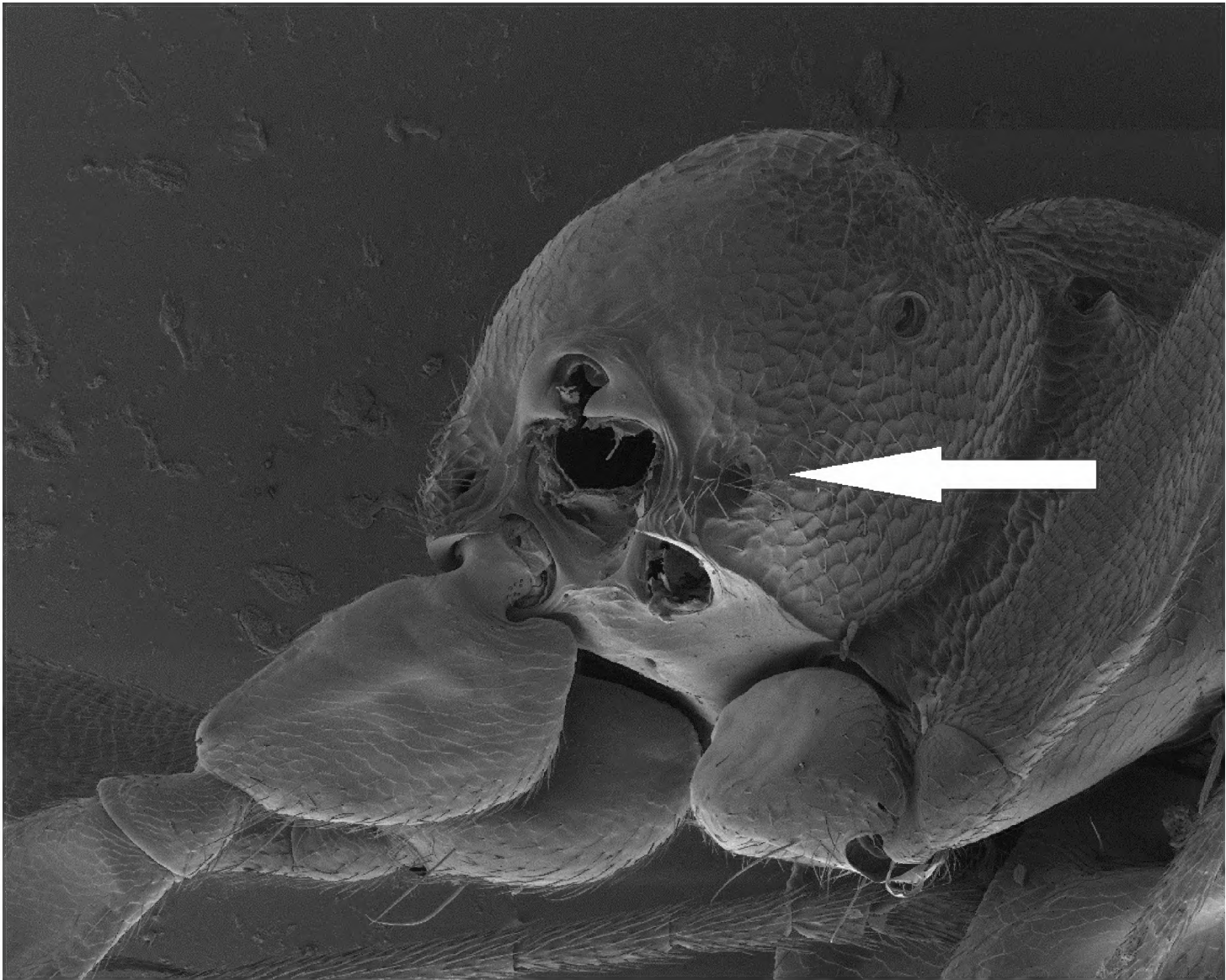


Figure 2. Metapleural gland opening of wingless *T. vitiensis* male.

Table 1. Means (in mm) and standard deviations of selected characteristics of *T. vitiensis* males with the significance of differences between winged and wingless morphs. Significant differences between winged and wingless forms are highlighted.

| Character | Winged males (n=6) | | | Wingless males (n=12) | | | p |
|-----------|--------------------|---------|---------|-----------------------|---------|---------|-------|
| | Mean | Minimum | Maximum | Mean | Minimum | Maximum | |
| HW | 0.61 | 0.57 | 0.63 | 0.59 | 0.52 | 0.83 | <0.05 |
| HL | 0.5 | 0.47 | 0.50 | 0.49 | 0.47 | 0.50 | >0.05 |
| ML | 0.98 | 0.92 | 1.02 | 0.85 | 0.82 | 0.90 | <0.01 |
| MH | 0.7 | 0.15 | 0.16 | 0.46 | 0.12 | 0.16 | <0.01 |
| SL | 0.15 | 0.65 | 0.75 | 0.14 | 0.42 | 0.51 | <0.05 |
| EW | 0.18 | 0.17 | 0.18 | 0.18 | 0.17 | 0.19 | >0.05 |
| EL | 0.26 | 0.25 | 0.27 | 0.23 | 0.20 | 0.25 | <0.01 |
| GW | 0.41 | 0.39 | 0.44 | 0.35 | 0.34 | 0.38 | <0.01 |

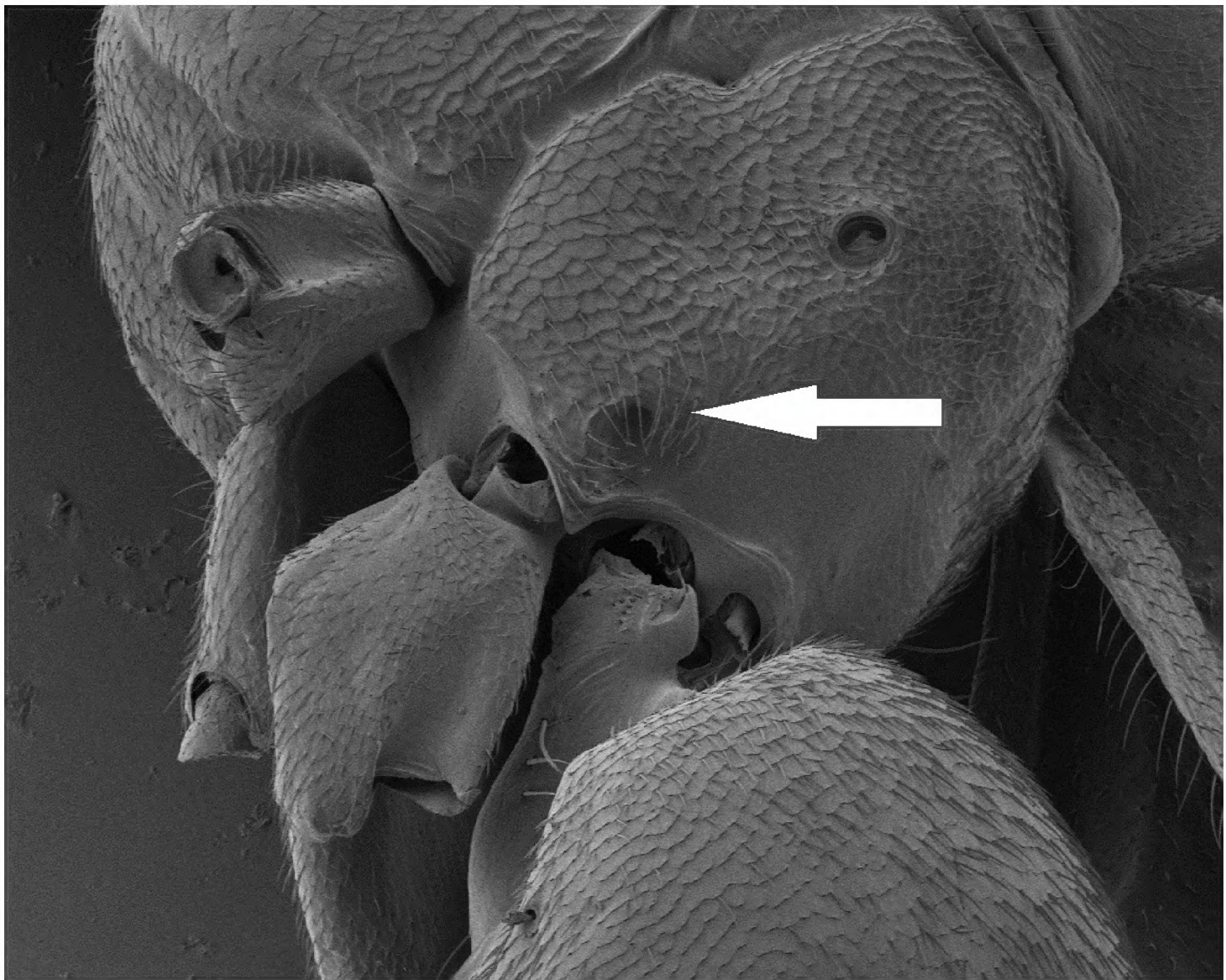


Figure 3. Metapleural gland opening of winged *T. vitiensis* male.

Metapleural gland openings are present in females as well as both winged and wingless males (Figs 2, 3).

Three wingless males show curious scape morphology: whereas normal scapes are straight, their scapes have a bulge on the distal end; thus, the whole scape resembles a hockey stick. Two males have modified both scapes and the third male has one normal and one modified scape (Fig. 4). The other morphological traits of these males do not seem to differ from males with normal scapes.

Behavior

In the botanical garden, apterous males were found during all visits (October, November, February, June). Winged males were captured only in the fall (one male was found in October and the other in November 2014 and another one in November 2015).

The preserved colony fragment from the botanical garden contained 67 workers, three intermorphic females and 14 wingless males. Additionally, several males, including two winged ones, were collected directly from the greenhouse and several lived in

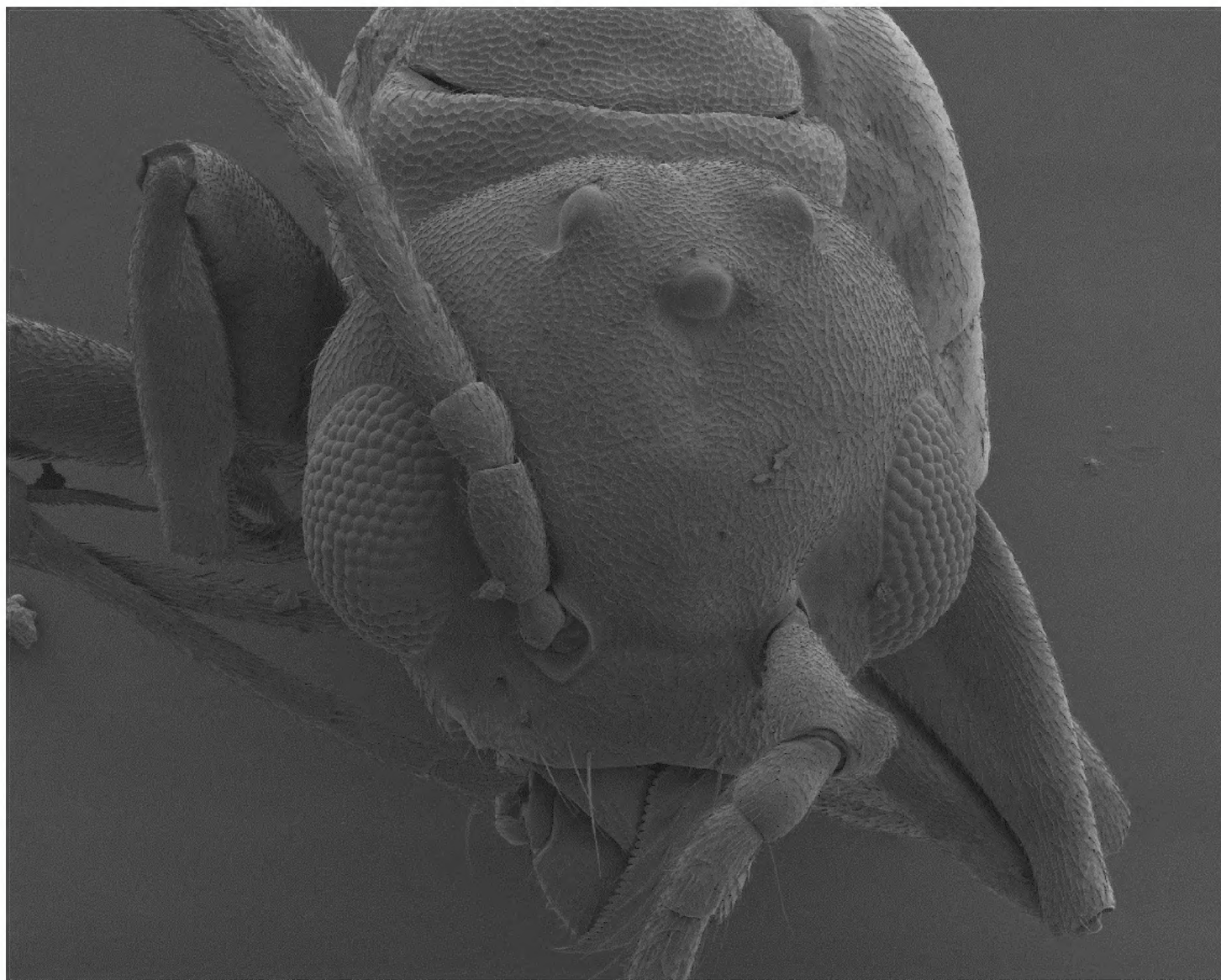


Figure 4. Head of a wingless *T. vitiensis* male with normal (left) and aberrant (right) scape.

the reared colony fragment. The preserved colony fragment from the zoological garden contained 499 workers, 80 intermorphic females (79 apterous and one brachypterous), eight winged queens and 24 males (21 winged and three wingless).

The reared colony fragment from the botanical garden contained about 100 apterous females and four apterous males with an amount of eggs, larvae and pupae at the time of collection. The colony fragment from the zoological garden contained about 30 apterous females and one apterous male with some brood. The ants from the botanical garden (fed by honey and pieces of insects) stopped breeding shortly after the collection and the brood disappeared in three weeks: female pupae matured but larvae and male pupae were probably eaten. Although eggs were present during six months of breeding, only one larva appeared but vanished soon.

During the breeding in captivity, no more than five males lived simultaneously in this colony fragment from the botanical garden. Males were not observed to carry or tend eggs or other juveniles. No aggressive interactions among these males were observed. Males behaved more actively than females and explored the arena more frequently. This behavior led to high male mortality, because two of them got stuck in the oil cover on the walls and one in the honey; no worker died in this way. All wingless

males died within two weeks after capturing the colony fragment or emerging from pupae, whereas the mortality of females was much lower (1–2 dead individuals per week). Also, during the search in the botanical garden, several wingless males were observed outside nests, walking on leaves and the ground.

Ants from the zoological garden (fed by Bhatkar and Whitcomb diet), four months since the start of breeding, still have brood of all stages but no new males are produced.

Discussion

Interestingly, the loss of wings is not connected with an absence of ocelli. The development of flight muscles and the size of the genitalia seem to be the main differences between the two types of males. In *T. brunneus*, mating between wingless and winged sexuals is probably impossible due to the big difference in the size of the genitalia (Ogata et al. 1996) – the average width of the genitalia of wingless males is almost two times smaller than that of winged males. A similar difference occurs in the genitalia width between winged and wingless females. Also in *T. vitiensis*, the difference in size of the genitalia of males of both types is significant. Because no winged females were measured, it is unclear whether female genitalia share the same pattern. However, the male genitalia size seems to be linked with the body size.

Both winged and wingless males have developed metapleural gland openings. Antimicrobial and antifungal metapleural gland secretion is an important component of ant immunity, but several other functions of these glands are also suggested (Yek and Mueller 2011). Metapleural glands are usually present in females but rarely in male ants, possibly because of the usually short life of ant males in the adult stage (Hölldobler and Engel-Siegel 1984, Yek and Mueller 2011). Until now, metapleural glands have been observed in males of only two species – *Dorymyrmex tener donisthorpei* (Santschi, 1936) and *Iridomyrmex purpureus* (Smith, 1858) – out of more than 700 species of the subfamily Dolichoderinae (Yek and Mueller 2011). It should be noted that the presence of metapleural gland openings does not imply the existence of a functional metapleural gland. The functionality and structure of metapleural glands in *T. vitiensis* are currently being studied (Billen and Pech, in prep.). Because *T. vitiensis* males (especially alate) seem not to live very long, the adaptive function of their metapleural glands, if present, is not clear (beside the high pressure of fungal and bacterial parasites in wet tropical habitats in general; but that would apply for many other tropical ant species as well). As the function of metapleural gland is poorly understood, all potential hypotheses are speculations.

The existence of two types of scapes in males is very interesting. Further research is needed to resolve whether there is a separate caste of male or teratological form.

Apterous males are probably present in colonies during the whole year, whereas the occurrence of winged males seems to be limited seasonally. The question is: If the amount of males can reach more than 10% of all adults in a nest, why have apterous

males not been observed until now? First, wingless males are very similar to females at first sight. Second, according to Yamauchi et al. (1991), the variation in the number of apterous males both inter-colonial and intra-colonial (among nests of the same polydomous colony) in *T. brunneus* is high and these males appear in the relatively small proportion of colonies in the field. The differences in the number of apterous males in our samples from the botanical and zoological gardens show that it is reality also in populations of *T. vitiensis*. Wingless males are clearly not always abundant. The diet of ants in the captivity could be another reason because ants are often fed by honey and dead insects as in case of Oettler and Heinze (2009) research of *T. vitiensis*. Using this diet, adults of *T. vitiensis* survive but do not breed.

Our observation supports the absence of aggressive male-to-male interaction in *Technomyrmex*. In contrast to wingless males in *Cardiocondyla* (e.g., Heinze and Hölldobler 1993) and *Hypoponera* (e.g., Bolton and Fisher 2011), which struggle with each other in an attempt to monopolize mating, *Technomyrmex* males were not observed fighting with each other (Yamauchi et al. 1991). Interestingly, six wingless and one winged male with amputated legs and antennae were discovered during the research in the botanical garden, located in one leaf about 1 m above the ground (3.xi.2014). All were immobilized but some of them were still alive. Additionally, at the other site, a *T. vitiensis* female was observed carrying and tossing away a badly injured apterous male. As male-to-male aggression is probably absent in *Technomyrmex*, the injuring and death of these males were most probably caused by intercolonial aggression. Fights among ants from different colonies are mentioned by Tsuji and Yamauchi (1994) in *T. brunneus*. One expects *T. vitiensis* to form one huge polydomous colony in the same greenhouse, but if several live individuals from another nest (captured at the same time in a banana tree about 4 m distant from the original site of the reared colony fragment) were added to the reared colony fragment, aggressive interactions among members of both nests were observed. This behavior (jerky lunges with open mandibles and pulling at appendages) ceased within two days. Thus, the males were probably killed by members of a more distant nest in the greenhouse.

The walking of wingless males outside nests implies the possibility of their extranidal mating with intermorphic females from another nest or colony and can weaken the intracolony inbreeding in *Technomyrmex* colonies.

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